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Differential germination strategies of native and introduced populations of the invasive species *Plantago virginica*

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Abstract

Germination strategies are critically important for the survival, establishment and spread of plant species. Although many plant traits related to invasiveness have been broadly studied, the earliest part of the life cycle, germination, has received relatively little attention. Here, we compared the germination patterns between native (North America) and introduced (China) populations of *Plantago virginica* for four consecutive years to examine whether there has been adaptive differentiation in germination traits and how these traits are related to local climatic conditions. We found that the introduced populations of *P. virginica* had significantly higher germination percentages and faster and shorter durations of germination than native populations. Critically, the native populations had a significantly larger proportion of seeds that stayed dormant in all four years, with only 60% of seeds germinating in year 1 (compared to >95% in introduced populations). These results demonstrate striking differences in germination strategies between native and introduced populations which may contribute to their successful invasion. Moreover, the germination strategy of *P. virginica* in their native range exhibited clear geographical variation across populations, with trends towards higher germination percentages at higher latitudes and lower annual mean temperatures and annual precipitation. In the introduced range, however, their germination strategies were more conserved, with less variation amongst populations, suggesting that *P. virginica* may have experienced strong selection for earlier life history characteristics. Our findings highlight the need to examine the role of rapid evolution of germination traits in facilitating plant invasion.

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Keywords
Adaptation, germination strategy, native and introduced populations, invasive species, *Plantago virginica*

Introduction

Invasive species have become a severe threat to terrestrial ecosystems and human society owing to their impacts on biodiversity, ecosystem functioning (Kolar and Lodge 2001) and economies (Strayer et al. 2006). Understanding the mechanisms that promote invasion success is critical for predicting the emergence and expansion of an invasion and determining strategies for mitigating their impacts (Kolar and Lodge 2001; Strayer 2012). Several decades of research has identified plant traits such as size, growth rate and competitive ability that often correlate with invasion success (van Kleunen et al. 2010). In contrast, the earliest part of the life cycle, germination, has received relatively little attention. (Udo et al. 2017; Gioria and Pyšek 2017).

As the first phase in the life cycle of plants, germination is pivotal for the establishment and expansion of populations, especially for annual species under competitive conditions (Donohue et al. 2010; Hirsch et al. 2012; Leiblein-Wild et al. 2014). Several germination characteristics have been found to be related to invasive potential (Baker 1974; Radford and Cousens 2000), but successful germination strategies may vary amongst ecosystems. For example, comparative experimental studies between invasive and non-invasive congeners under experimental conditions showed that invaders tended to germinate earlier and took shorter time to reach the highest germination percentages (Muñoz and Ackerman 2011). In an Argentina desert community where the native annual flora is mainly composed of summer annual species, the late germination niche of the alien winter annual grass *Schismus barbatus* contributes to its successful invasion (Pucheta et al. 2011). In California grasslands, earlier germination phenology has been shown to yield competitive advantages for invasive species (Godoy and Levine 2014).

Similar to interspecific comparisons, examining the differentiation in germination patterns of an invasive species between its native and introduced ranges can also provide insights into the ecological and evolutionary mechanisms of invasion. Several studies have shown that seeds, originating from introduced populations, germinated at greater percentage, earlier and/or faster (Blair and Wolfe 2004; Erfmeier and Bruelheide 2005; Maron et al. 2007). Studies of intraspecific variation in germination can help explain species' range expansions (Blair and Wolfe 2004; Erfmeier and Bruelheide 2005; Kudoh et al. 2007; Maron et al. 2007).

In addition to seasonal timing of germination, seed dormancy is also an important component of a species temporal niche and life history strategy (Baskin and Baskin 2014). However, relatively few studies have examined how seed dormancy strategies could contribute to the success of invasive species. Kudoh et al. (2007) found that Japanese (introduced) populations of *Cardamine hirsuta* exhibited stronger initial dormancy and more persistent seed banks than European (native) populations, both of which can increase the probability of survival in the novel range. An opposite pattern

of seed dormancy was reported for introduced populations of *Ulex europaeus* which showed less physical dormancy, perhaps selected by decreased seed predation in the introduced range (Udo et al. 2017).

The variation in seed germination and dormancy could be driven by geographical variation in environmental factors, such as temperature and precipitation (Blair and Wolfe 2004; Sax et al. 2007) and further lead to population differentiation. For example, germination timing and rates of *Campanula americana* showed adaptive responses to local temperatures across its latitudinal range (Zettlemoyer et al. 2017). The rapid adaptation of introduced plants to the local environments plays a fundamental role in the expansion of species' geographical ranges and invasion success in introduced ranges. Hence, understanding intraspecific variation in germination characteristics across geographic and environmental gradients is important for interpreting invasion mechanisms and predicting the distribution of exotic species in future.

The goal of this study was to use a set of four-year germination experiments to build a better understanding of how seed germination traits may contribute to plant invasiveness. We used, as a case study, *Plantago virginica*, a species native to North America that has invaded China (Wang et al. 2015). Specifically, we compared germination percentages, timing and speed and rates of dormancy of seeds collected from native and introduced populations under controlled experimental conditions. We also used widespread seed collection sites in order to evaluate whether germination characteristics exhibit adaptation to local climatic conditions. The germination experiments were conducted for consecutive four years to test how seed dormancy, a critical part of the plant species' life history strategy, is different in the introduced versus native range.

Materials and methods

Study Species

Plantago virginica is an annual herb native to eastern North America that was introduced by accident and first reported in Jiangxi Province in the southeast of China in 1951. Since that time, it has spread extensively to eastern and southern China (Guo et al. 1996; Wang et al. 2015) and, more recently, north and west in Hunan, Henan and Chongqing Provinces (Fang et al. 2004; Guo et al. 1996; Wang 2016). The species' primary habitats in the introduced range include abandoned farmlands, orchards and lawns.

P. virginica is a winter annual. It germinates in the autumn, grows vegetatively through the winter and flowers, sets seeds and dies in the following spring and summer. It consists of a rosette of basal leaves, from which one or more cylindrical flowering spikes develop, densely covered with small flowers and their bracts. The species produces dimorphic flowers that exhibit a mixed mating system: cleistogamous (permanently closed, self-pollinated, i.e. selfing) and chasmogamous (wind or insect-pollinated, i.e. outcrossing) flowers (Xu et al. 2017). One individual usually produces

200–500 seeds (Guo et al. 1996). The seeds are often dispersed by animals or humans (Fang et al. 2004). Due to its strong reproductive ability and fast dispersal, *P. virginica* in the introduced range has caused substantial effects on native species and ecosystems and was listed as an invasive plant by China (Database of Invasive Alien Species in China (http://www.chinaias.cn).

Seed collections

Seeds for this study were collected in 2012 from 12 native (USA) and 10 introduced (China) populations (Fig. 1, Suppl. material 1: Table S1). The seeds from each population were collected from at least 30 individuals representing different maternal families (growing at least 1 m apart) and placed in separate paper envelopes and stored at 4 °C before the experiments.

Germination experiments

Germination trials were conducted with seeds from the same initial seed collection for four consecutive years (2012–2015), in order to compare the effect of seed dormancy amongst populations (see populations we used in each experiment in the Suppl. material 1: Table S1). The first experiment was in autumn 2012 in Shanghai, China, consisting of 10 native and 10 introduced populations, with 6 replicates per population (a Petri dish containing 50 seeds was the replicate). The 50 seeds of each replicate were weighed to the nearest 0.0001 g. The second experiment was conducted in spring 2013 in Statesboro, GA, USA and used 20 seeds from each of 10 native and 10 introduced populations. The final two experiments were conducted in autumn 2014 and 2015, in Nanjing, China with each experiment comprising of six native and six introduced populations and each population containing 25 replicates and 30 seeds per replicate. In 2015, additional 5 replicates were used to investigate the proportion of mouldy seeds in both native and introduced populations. All the seeds representing each population were thoroughly mixed while being selected for germination.

For each germination trial, seeds were placed on moistened filter papers in Petri dishes and incubated in illumination incubators with a photoperiod of 12 h cold white light and 12 h darkness under 25 °C. Petri dishes were watered daily and the number of germinated seeds was counted as their visible radicles reached a length of 2 mm. Since a preliminary experiment revealed that the seeds of *P. virginica* typically germinate in two weeks, the present experiments lasted between 2–3 weeks, allowing one week to ensure that no more seeds germinated. The germination percentage (the proportion of germinated seeds), the days to germination (the day of the first occurrence of germination in each replicate) and the duration of germination (the period from the first to the last seed germinating) were calculated.

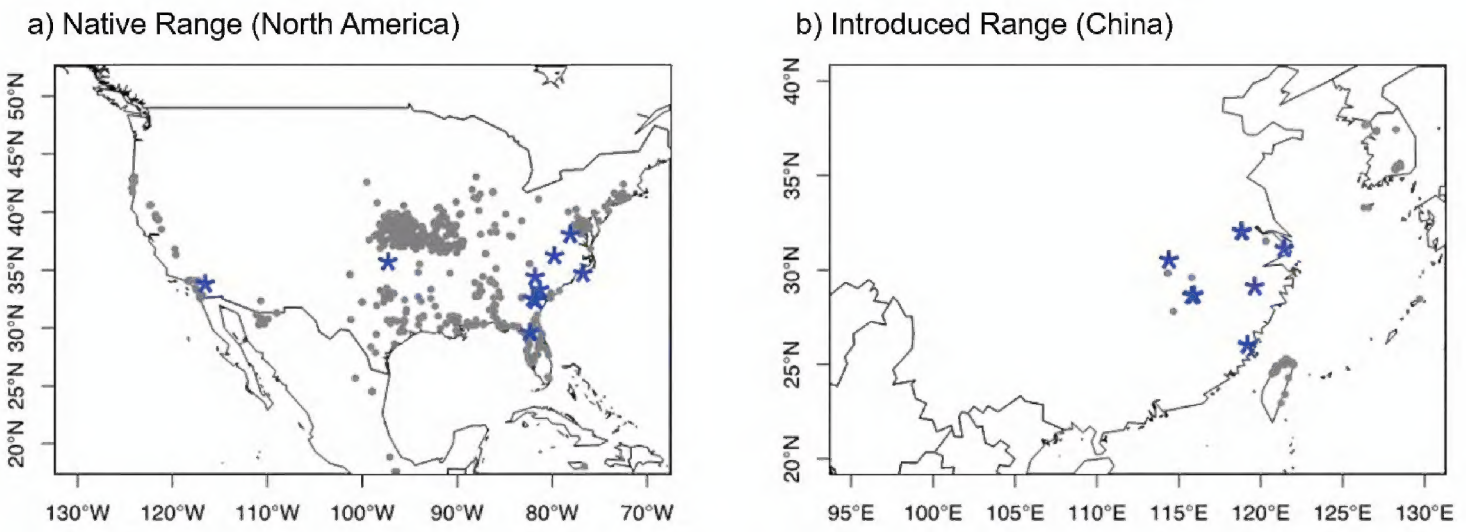
a) Native Range (North America)
b) Introduced Range (China)
20°N 25°N 30°N 35°N 40°N 45°N 50°N
130°W 120°W 110°W 100°W 90°W 80°W 70°W
20°N 25°N 30°N 35°N 40°N
95°E 100°E 105°E 110°E 115°E 120°E 125°E 130°E

Figure 1. Locations of *P. virginica* in the native range (**a**) and introduced range (**b**). Grey dots represent GBIF data as a background representation of the species' approximate range and the blue asterisks show the locations of populations sampled for seeds.

Statistical analyses

Data of germination characteristics were analysed by generalised linear mixed models (GLMM) and mixed-effects Cox models, with region and year as fixed factors and population within region as a random factor. We validated the use of GLMMs with the restricted maximum likelihood (Laplace Approximation) estimation method (REML) based on the normalised scores of standardised residual deviance of response variables: germination percentage and duration of germination. The level of significance of each fixed factor was determined by an *F*-ratio test. The analyses were performed with statistical package "lme4" in R. For the analysis of days to germination, we used a mixed-effects Cox model fit by maximum likelihood to examine the differences in timing of germination between native and introduced regions and amongst years. The level of significance of each fixed factor was determined using χ^2-test. The analysis was performed with statistical package "coxme" in R. We also examined the differences in germination characteristics (germination percentages, days to germination and duration of germination) of each region amongst years using the least significant difference (LSD) test. Due to the lack of data on "days to germination" and "duration of germination" in 2013, data from three years (2012, 2014 and 2015) of these two variables were used in the generalised linear mixed models, mixed effects Cox model and the LSD test. Since seed mass may affect the germination characteristics, especially germination percentage, data for germination characteristics in our first experiment (2012) were independently analysed by GLMM and mixed-effects Cox models, with region as a fixed factor and seed mass and population within region as random factors, to test for the effects of region while controlling for seed mass. The differences in proportion of mouldy seeds between native and introduced regions were tested using another generalised linear mixed model, with region as a fixed factor and population as a random factor.

Relationships between climate and germination characteristics were analysed using GLMMs. Monthly mean temperature and precipitation values for each sampling site were extracted using QCIS 2.18 (Becker et al. 2016), from WorldClim 2.0, a global climate database (www.worldclim.org) with a spatial resolution of 1 km. Mean annual temperature and precipitation of each site were used to test for relationships between germination characteristics of seeds and environmental conditions using mixed models that accounted for population as a random effect and estimated temperature, precipitation and latitude as fixed effects. Models were fitted using all covariates alone and in combination as a multiple regression, as well as allowing for interaction between temperature and precipitation. Model comparison was conducted using AIC.

Results

Germination characteristics of native and introduced populations

Introduced populations of *P. virginica* displayed significantly higher germination percentages (96.76 ± 0.36) than native populations (84.21 ± 1.29) in the four-year experiments (Fig. 2a) and germination percentages were significantly different amongst years ($P < 0.001$; Table 1; Fig. 3a). For native populations, germination percentage increased through the four years (from 61.14 ± 5.00 in 2012 to 94.24 ± 1.00 in 2015). For introduced populations, there was no such significant change in germination over time (Fig. 3a).

Seeds from introduced populations started to germinate significantly earlier than those of native populations in all three years ($P < 0.001$; Table 1; Fig. 3b). The days to germination differed significantly amongst years ($P < 0.001$; Table 1) and gradually got shorter in later years for both native and introduced populations (7.37 ± 0.07 to 4.14 ± 0.07 and 7.00 ± 0.00 to 3.44 ± 0.07, respectively; Fig. 3b).

Native populations displayed longer durations of germination than introduced populations in all years (Table 1; Fig. 2c), but the magnitude of this difference varied amongst years (Table 1; Fig. 3c). The duration of germination of native populations diminished over years (from 3.24 ± 0.25 to 2.60 ± 0.11) (Fig. 3c).

The impact of seed mass on germination characteristics

There was no difference in seed mass between the native and introduced ranges, but seed mass was significantly different amongst populations within each region (See Suppl. material 2: Figure S1). Overall germination percentages, the days to germination and the duration of germination were all significantly different between regions, even when controlling for the effects of seed mass (Table 2).

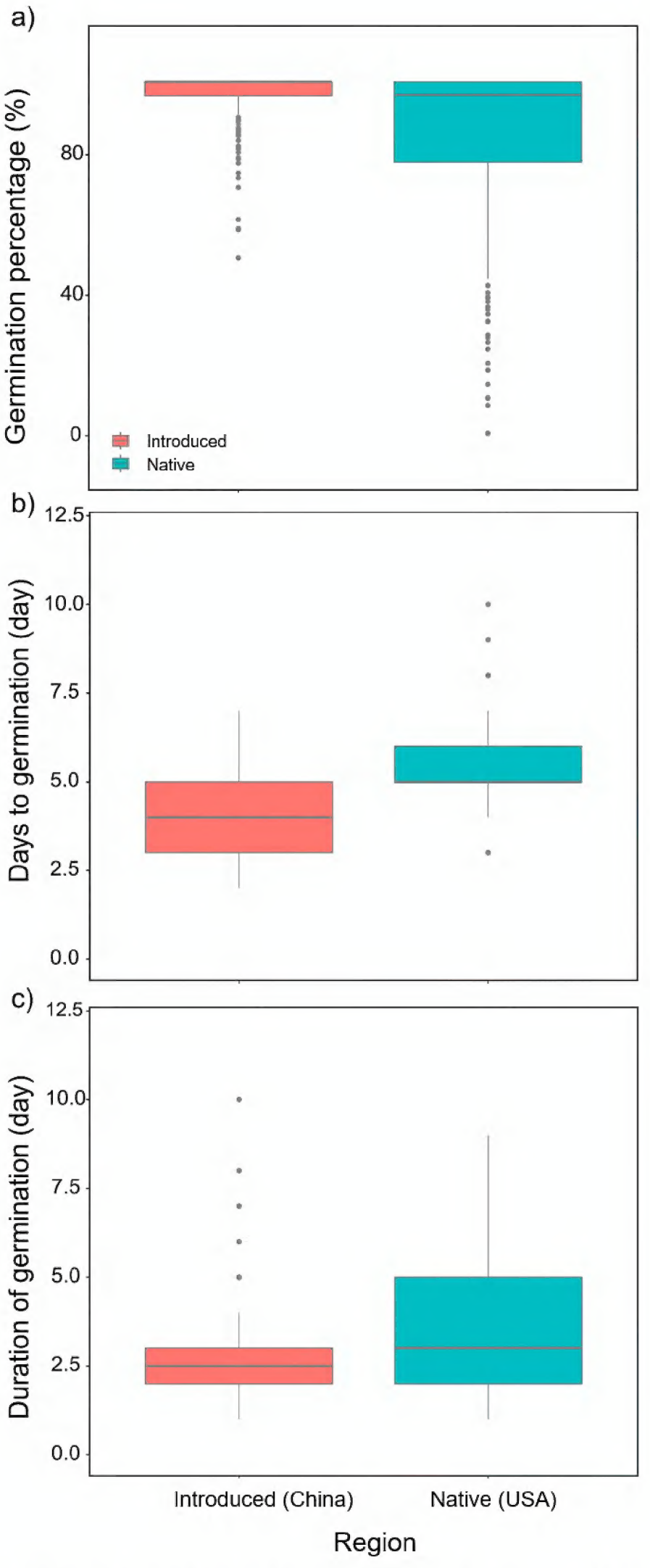

Figure 2. Box plots of introduced (China) and native (USA) populations of *Plantago virginica* across years: **a** germination percentage **b** days to germination **c** duration of germination.

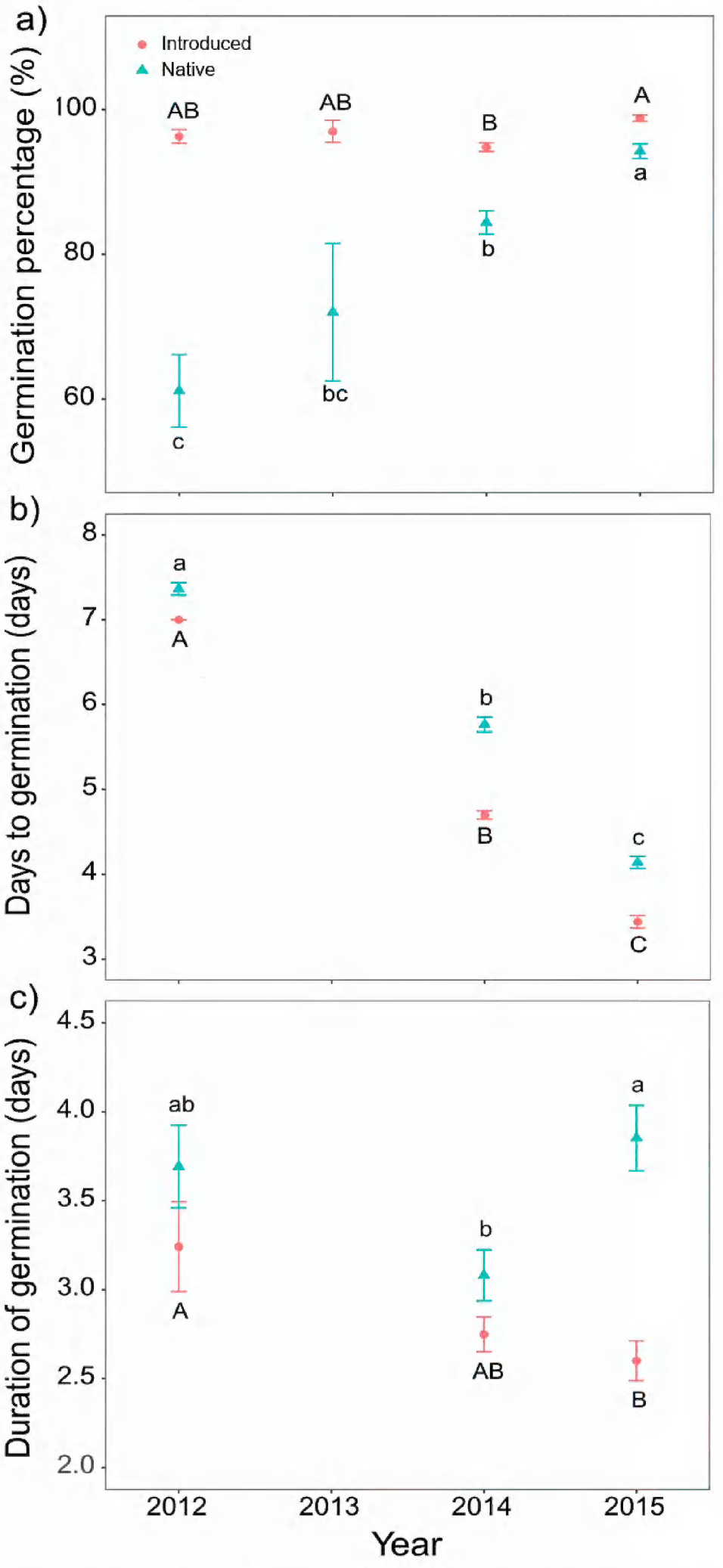

Figure 3. Mean trait values (± SE) of native (USA) (blue triangles) and introduced (China) (red symbols) populations of *Plantago virginica*: **a** germination percentage **b** days to germination **c** duration of germination. Days to germination and duration of germination were not measured in 2013. Within each panel, means labelled with the same letter (capital: introduced populations; lower case: native populations) do not differ at $P = 0.05$ based on LSD test.

Table 1. Summary of generalised linear mixed models analyses of germination percentage and duration of germination and mixed-effects Cox model of days to germination of *P. virginica* from introduced (China) and native (USA) regions.

	Germination percentage (%)			**Days to germination (d)**		**Duration of germination (d)**		
Fixed effects	df	Residual df	*F*	df	χ^2	df	Residual df	*F*
Region	1	718	7.096*	1	193.862***	1	694	18.328***
Year	3	718	27.26***	2	534.160***	2	694	5.342**
Region ×Year	3	718	21.02***	2	20.868***	2	694	4.880**
Random effects			SD		SD			SD
Population (Region)			0.962		0.805			0.060

Variables of germination percentage and duration of germination were analysed with generalised mixed-effects models and the fixed effects were tested with numerical approximations of the *F*-statistic. Variables of days to germination were analysed with a mixed-effects Cox model and the fixed effects were tested with deviance differences as χ^2-statistic. † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 2. Summary of generalised linear mixed models analyses of germination percentage and duration of germination and mixed-effects Cox model of days to germination of *P. virginica* from introduced (China) and native (USA) regions in the experiment conducted in 2012.

	Germination percentage (%)			**Days to germination (d)**		**Duration of germination (d)**		
Fixed effects	df	Residual df	*F*	df	χ^2	df	Residual df	*F*
Region	1	116	3.9801*	1	124.74***	1	110	1.0709*
Random effects			SD		SD			SD
Seed mass			2.4186		0.0132			0.1220
Population (Region)			1.0650		1.3737			0.1741

Variables of germination percentage and duration of germination were analysed with generalised mixed-effects models and the fixed effects were tested with numerical approximations of the *F*-statistic. Variables of days to germination were analysed with a mixed-effects Cox model and the fixed effects were tested with deviance differences as χ^2-statistic. † $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

The proportion of mouldy seeds in native and introduced populations

The proportion of mouldy seeds in introduced populations (22.53 ± 7.99 (%)) was significantly higher than in native ones (4.80 ± 1.70 (%)) after being subjected to a four-year storage period (Suppl. material 3: Figure S2).

Relationships between germination characteristics and environmental variables

None of the germination characteristics (germination percentage, days-to-germination, nor germination duration) was significantly related to mean annual temperature, precipitation and latitude (Suppl. material 5: Figure S4; all $P > 0.1$). Lowest AIC values supported models only including population-level random effects. However, there was significantly more variability in germination percentages amongst populations in the native range compared to the introduced range, suggesting greater population differentiation (std = 1.55 in native range and std < 0.1 in the introduced range).

Discussion

The potential importance of germination characteristics for biological invasions has been hypothesised for decades (Baker 1974) and, because of their crucial consequences for fitness, germination traits are thought to undergo strong environmental selection (Cohen 1966; Donohue et al. 2005; Hierro et al. 2009; Venable 2007). Nonetheless, few comparative studies of invaded and native ranges have been conducted. Here, we found that the introduced populations of *P. virginica* had significantly higher germination percentages and faster and shorter durations of germination than native populations. Specifically, the seeds of introduced populations germinated more rapidly and reached a higher germination percentage in a shorter time, whereas the seeds of native populations germinated more slowly and took a longer time to complete germination. Critically, the native populations had a significantly larger proportion of seeds that stayed dormant in all four years, with only 60% of seeds germinating in year 1 (compared to >95% in introduced populations). These results demonstrate striking differences in germination strategies between native and introduced populations which may contribute to their successful invasion.

Germination percentages, speed and timing

Recent studies have reported that the introduced populations can have higher germination percentages than native populations, often arguing that the higher germination percentages in many cases were due to higher seed mass in invasive populations (Beckmann et al. 2011; Leiblein-Wild et al. 2014). In this study, we also found that the germination percentages in introduced populations were higher, but the differences in germination percentages between regions were independent of seed mass.

The timing and speed of germination play important roles in determining the successful establishment of exotic species when they arrive in novel environments (Baskin and Baskin 2014; Donohue et al. 2010; Gioria and Pyšek 2017; Gioria et al. 2018). Rapid germination gives plants a size advantage in early season (van Kleunen and Johnson 2007) and the subsequent asymmetric competition may then thwart establishment or reduce growth and reproduction of the ones with later germination (Schlaepfer et al. 2010; Weiner and Thomas 1986). For example, it has been reported that the seeds of introduced populations of *Ambrosia artemisiifolia*, *Rhododendron ponticum* and *Ulmus pumila* germinated earlier and faster than those of native populations (Erfmeier and Bruelheide 2005; Hirsch et al. 2012; Leiblein-Wild et al. 2014). Such pattern was also found in other species such as *Eupatorium adenophorum* (Li and Feng 2009), *Echium* and *Verbascum* species (Hock et al. 2015). Our results are consistent with these findings, showing that seeds of introduced populations germinated earlier and faster than those of native populations. The enhanced performance in the introduced populations of *P. virginica* may be explained by the Evolution of Increased

Competitive Ability hypothesis (EICA). Due to a lack of native enemies, the introduced plants may reallocate resources from defence mechanisms into growth and gain a greater fitness than their native counterparts (Blossey and Nötzold 1995; Callaway and Ridenour 2004; Joshi and Vrieling 2005). Although the introduced plants always performed better than native ones, we cannot rule out other mechanisms (such as phenotypic plasticity) due to the lack of direct evidence showing the rapid evolution of competition ability of plants in introduced populations.

Furthermore, genetic-based variation in germination has recently been demonstrated in invasive species. Based on a quantitative trait-loci analysis, Huang et al. (2010) showed that germination phenology of *Arabidopsis thaliana* was linked to particular regions on chromosomes. In addition, other factors such as founder effects, random genetic drift and maternal effects could also be responsible for differences in germination traits between native and introduced regions. Therefore, it remains an open question in most cases whether differences in germination percentages have been selected by the environments in introduced region and therefore are an important determinant of invasiveness (Gioria et al. 2018) or are a by-product of the genetic bottleneck and/or random chance associated with the invasion process (Sakai et al. 2001).

Seed dormancy

Amongst other germination characteristics, seed dormancy represents an important component of a germination strategy (Baskin and Baskin 2014) and is often a bet-hedging and/or risk-reducing strategy in temporally unfavourable conditions and/or unpredictable environments (Venable 2007; Venable and Brown 1988). The strategy of low germination percentage with deep dormancy can reduce the risk of extinction during unfavourable conditions. In our study, we found that seeds of native populations had significantly deeper dormancy, i.e. the germination percentage of seeds collected from native populations increased with storage time. This result suggests that the conditions of plant growth in introduced populations are more favourable or the seedlings in introduced populations had higher ability to tolerate unsuitable conditions (Gioria et al. 2018). Higher tolerance of seedlings with higher germination percentage and speed can further facilitate the success of invasion (Leiblein-Wild et al. 2014).

Alternatively, high germination percentages can serve as an escape from unfavourable conditions in the seed bank. If predators or pathogens attack seeds more than seedlings, rapid germination rather than dormancy could be advantageous (Baskin and Baskin 2014; Xiao et al. 2007). Indeed, we investigated the proportion of mouldy seeds after storage for four years and found that the proportion of mouldy seeds was higher in introduced populations than in native ones (See Suppl. material 3: Figure S2), which is consistent with previous reports (Baskin and Baskin 2014).

Geographical differentiation in seed germination

Geographical variation in local adaptation to climates or environments can enable a species to inhabit a large ecological breadth and range. For instance, Meyer et al. (1995) found that more widely distributed *Penstemon* species exhibited more variable germination patterns across their range, suggesting that ecotypic differentiation in germination itself may contribute to the geographic range of widespread species. A recent study also reported a geographical pattern of seed germination in *Gladiolus gueinzii* (Tabassum and Leishman 2018). It found that the seeds from the range edge populations had significantly faster germination times and greater dispersal ability which may be a key factor in promoting further range expansion of this species (Tabassum and Leishman 2018). Alternatively, a wide germination niche of species could simply result from very broad germination requirements for all populations of that species (Baskin and Baskin 2014; Donohue et al. 2010). In at least one case study, species with a wider range of germination temperatures also had larger geographic ranges (Brändle et al. 2003).

In the present study, the germination strategy of *P. virginica* in their native range exhibited clear geographical variations across populations, with trends towards higher germination percentages at higher latitudes and lower annual mean temperatures and annual precipitation (Suppl. material 5: Figure S4). Although these relationships were not statistically significant, the clear differences amongst populations suggest selection for germination strategies due to other local habitat factors. In the introduced range, however, their germination strategies were more conserved, with less variation amongst populations, suggesting that *P. virginica* may have experienced strong selection for earlier life history characteristics and /or not enough time for subsequent evolution to occur.

The more limited range of germination traits in introduced populations may also be ascribed to the more homogenous genetic background and lower genetic loads than in native populations caused by the genetic bottleneck and Allee effect during the range expansion (Sakai et al. 2001). Thus, it is possible that lower genetic diversity of *P. virginica* in the introduced range may have led to weaker responses to geographical variation in environmental factors and further limited the expansion of distribution range in a short invasive history (Xu et al. 2017). Moreover, the sampling range in China was not as broad as that in the U.S., which may influence these inferences about population differentiation, but these sampling sites represented almost all habitats across most of the distribution of *P. virginica* in China.

Conclusions

There was significant differentiation in germination strategies and dormancy patterns between native and introduced populations in *P. virginica*. Seeds of introduced populations exhibited less dormancy and higher germination percentage and germinated earlier and faster than those of native populations. The germination

strategy of *P. virginica* in their native range exhibited clear geographical variations across populations, with trends towards higher germination percentages at higher latitudes and lower annual mean temperatures and annual precipitation. In the introduced range, however, their germination strategies were more conserved, with less variation amongst populations, suggesting that *P. virginica* may have experienced strong selection for earlier life history characteristics. These differences in seed germination characteristics are likely to impact the individual plant fitness, biotic interactions, as well as the species' success with invasion. Our findings highlight the need to further examine the role of rapid evolution of germination traits in facilitating plant invasions.

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Supplementary material 1

Table S1. Source populations of *P. virginica* seeds used in germination experiments
Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu
Data type: species data
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Link: https://doi.org/10.3897/neobiota.43.30392.suppl1

Supplementary material 2

Figure S1. Box plots of seed mass
Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu
Data type: statistical data
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Link: https://doi.org/10.3897/neobiota.43.30392.suppl2

Supplementary material 3

Figure S2. Proportion of moldy seeds
Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu
Data type: species data
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Link: https://doi.org/10.3897/neobiota.43.30392.suppl3

Supplementary material 4

Figure S3. Photos of introduced population of *P. virginica*

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu

Data type: media

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Supplementary material 5

Figure S4. Relationships between the germination traits and environmental variables

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu

Data type: statistical data

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Link: https://doi.org/10.3897/neobiota.43.30392.suppl6

Supplementary material 6

Coordinates

Authors: Xinyu Xu, Lorne Wolfe, Jeffrey Diez, Yi Zheng, Hui Guo, Shuijin Hu

Data type: occurrence

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